

PHOTOSYNTHETIC PRODUCTION BY THE CORAL REEF ANEMONE, *LEBRUNIA CORALLIGENS* WILSON, AND BEHAVIORAL CORRELATES OF TWO NUTRITIONAL STRATEGIES

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ABSTRACT

The coral reef anemone *Lebrunia coralligens* Wilson bears, in addition to its lanceolate, feeding tentacles, lobate pseudotentacles which are shown to be photosynthetic organs. Anemones exposed to light demonstrate a net oxygen production and, when incubated in $\text{NaH}^{14}\text{CO}_3$ in the light, incorporate ^{14}C into the zooxanthellae and animal tissue.

Diurnal rhythms of pseudotentacle expansion and contraction are under the control of ambient light but are modified by the animal's nutritional status. Unfed animals utilize their lobate pseudotentacles to obtain the maximum nutritional uptake by autotrophy while fed animals reduce their autotrophic intake. However, lanceolate tentacle expansion is primarily a feeding response and is augmented by a higher nutritional state. It is concluded that anemone behavior is an expression of the two nutritional strategies.

INTRODUCTION

Lebrunia coralligens Wilson is a small cryptic anthozoan which occupies cavities in dead and living coral rock (Wilson, 1890; Gladfelter, 1975). In addition to its lanceolate feeding tentacles, *L. coralligens* bears large, lobate, auxilliary extensions of the column termed pseudotentacles (Hyman, 1940). According to Gladfelter (1975) and Sebens and De Riemer (1977), the lanceolate tentacles are expanded during the night, whereas the lobate pseudotentacles are expanded during the day; the latter contain 20 to 30 times more zooxanthellae than do the true tentacles. These diurnal cycles of expansion and contraction, coupled with the presence of a large number of zooxanthellae in the pseudotentacles, have led the latter authors to conclude that *L. coralligens* is capable of both autotrophic and heterotrophic modes of nutrition.

The purpose of the present study was to confirm experimentally that the lobate pseudotentacles of *L. coralligens* are specialized photosynthetic organs, to measure their rate of production, and to determine how the two nutritional strategies may be integrated with polyp behavior.

MATERIAL AND METHODS

Specimens of *Lebrunia coralligens* were obtained from within rock surfaces on the fringing reefs at Barbados, West Indies (Lewis, 1960). Broken rock fragments were carried to the laboratory in sea water and the anemones carefully removed and transferred to clean glass dishes in which the water was changed twice daily. Living specimens were maintained in the laboratory for as long as two months in this manner.

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Specimens used for histological study were first incubated for 12 h in light or darkness in 350 ml of sea water to which approximately 20 μC of $\text{NaH}^{14}\text{CO}_3$ had been added, preserved in Bouin's fixative, and transferred to 70% ethanol. After imbedding in paraffin blocks, samples were sectioned at eight microns, mounted on slides smeared with albumin, and stained with hematoxylin. Slides prepared for tissue radiography were dipped in Kodak nuclear track emulsion (type N_2B_2 , 1:1 emulsion:water mixture) and exposed for 10 days at 5°C. Exposed slides were developed in Kodak D-19 developer, fixed in Kodak rapid fixer, and post stained with Eosin.

To measure respiration and photosynthetic activity, anemones were incubated in darkened and light glass, snap cap vials (60 ml) for two hours (between 1100 and 1300 h). This midday period was reported to be the time of maximum lobate tentacle expansion by Gladfelter (1975) and was probably within the period of maximum photosynthesis (Fricke and Vareschi, 1982). Control vials contained no anemones. Because of the small volume of the vials, changes in oxygen concentration in the vials were determined by the following modification of the Winkler method. Twenty ml of water were withdrawn from the incubation vessel into a glass syringe. The Winkler chemicals (0.1 ml manganous sulphate, 0.1 ml alkaline iodate, and 0.2 ml sulfuric acid) were dispensed into the sampling syringe and the sample was titrated against 0.01 *N* sodium thiosulphate with a microburet. To test for accuracy, the method was compared with an unmodified Winkler technique (Strickland and Parsons, 1965). Results differed by <5%.

Observations on diurnal rhythms of tentacle expansion were conducted over periods of seven days by arrangement of six groups of twenty individuals each as follows; (a) anemones (fed on the first and fourth days) exposed to a light/dark cycle of 12 h light from 0600 to 1800, and 12 h dark from 1800 to 0600 h; (b) anemones (fed on the first and fourth days) exposed to a reverse light/dark cycle of 12 h dark from 0600 to 1800 h, and 12 h light from 1800 to 0600 h; (c) anemones exposed to continuous light with daily feeding; (d) anemones exposed to continuous light with no feeding; (e) anemones exposed to continuous darkness with daily feeding; and (f) anemones exposed to continuous darkness with no feeding.

During the light/dark experiments, animals were contained in glass finger-bowls (350 ml) immersed in a water table with flowing sea water. Water in the bowls was changed twice daily. Fragments (1–2 mm³) of fresh fish muscle were offered as food. In the light experiments, animals were exposed to a pair of Grolux fluorescent lamps (300 lumens/m²) while dark bowls were covered with aluminum foil. The experimental light intensity chosen was within the range found by Gladfelter (1975) to elicit maximum lobate tentacle expansion. Randomly selected dark bowls were inspected under reduced light twice during the night and three times during the day, by briefly (<10 s) lifting the foil covering. Anemones were not observed to react to such brief exposure; Pearse (1974) reported a similar lack of response in the anemone *Anthopleura elegantissima* under the same treatment. Light bowls were inspected at two hourly intervals during the day and twice at night. As with the anemone *Anthopleura elegantissima* (Pearse, 1974), recording of expansion and contraction was simplified by the fact that the majority of anemones were either fully expanded or fully contracted under experimental conditions and arbitrary decisions were necessary only occasionally.

RESULTS

Larvae and juveniles

Planulae larvae of *Lebrunia coralligens* were released at irregular intervals in May and June. A typical larva was 1 mm in length and 0.5 mm diameter at the apical

end. In the laboratory, larvae were negatively phototropic, showed aggregated settlement behavior, and settled most frequently around the bases of the adults. Up to 50 planulae were released from a single adult. The planulae contained zooxanthellae arranged in longitudinal rows, bore eight apical white patches (the precursors of the first set of tentacles), and could swim slowly in a spiral fashion.

Settlement and metamorphosis occurred in most cases within 24 h and *Edwardsia* stage juveniles with eight tentacles were produced. Additional juvenile tentacles subsequently developed in several rows and were intermittently expanded during both day and night. Lobate pseudotentacles did not develop until about six weeks later. A six-week development sequence is shown in Figure 1.

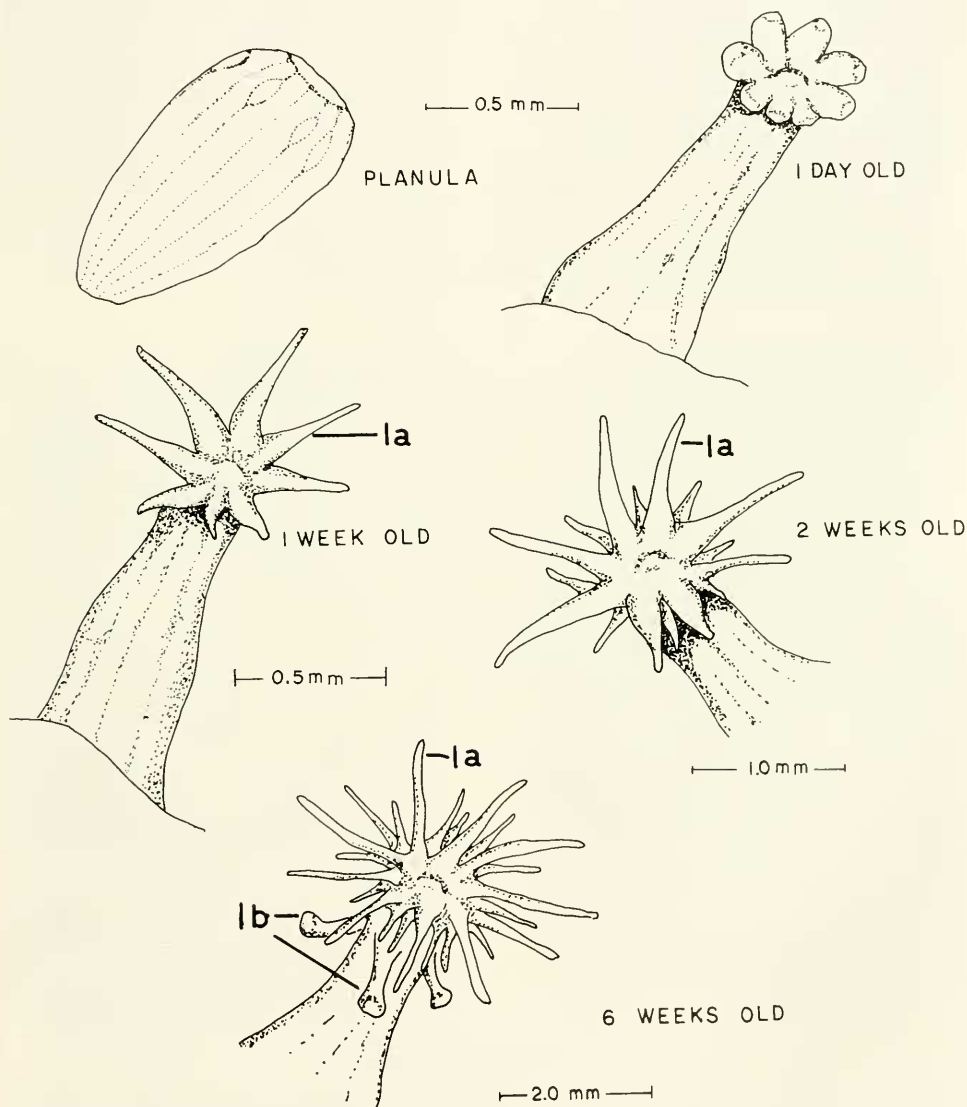


FIGURE 1. A six week development sequence of planula larva and juveniles of *Lebrunia coralligens*. 1a—lanceolate tentacle, 1b—lobate tentacle.

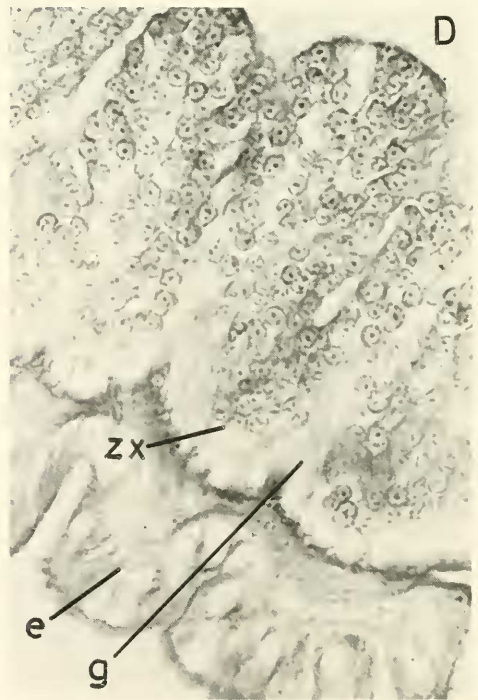
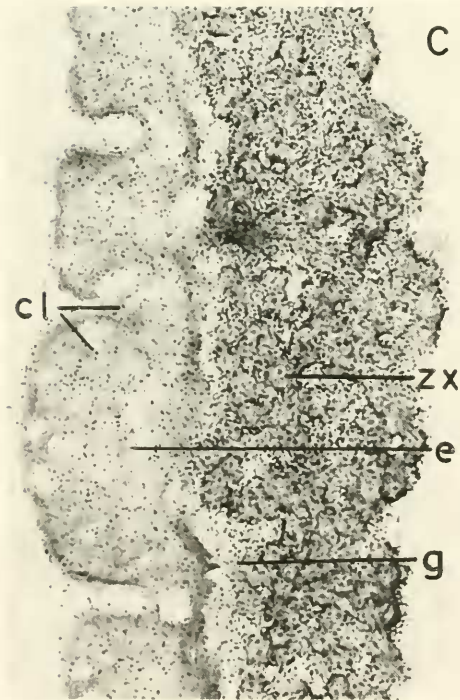
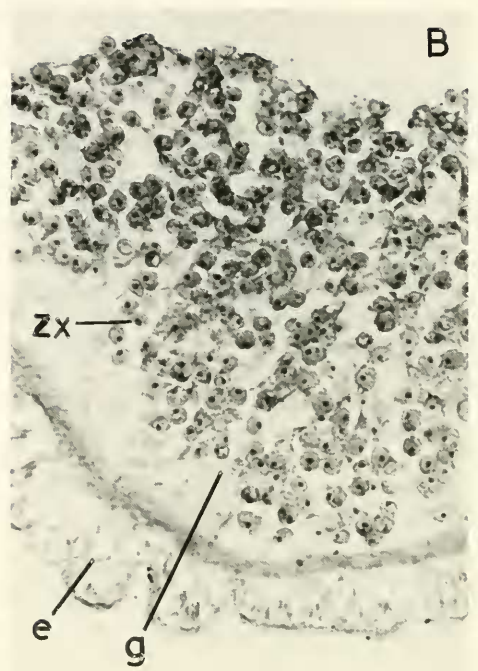
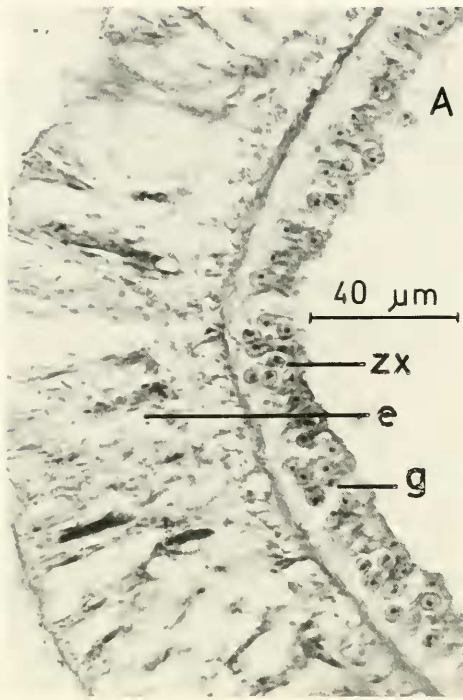


FIGURE 2. Cross sections of lanceolate feeding tentacles and lobate pseudotentacles of *Lebrunia coralligens*. A—section of lanceolate tentacle showing thin layer of zooxanthellae. B—section of lobate tentacle showing dense layer of zooxanthellae. C—autoradiograph of lobate tentacle incubated in light showing dense labelling by ^{14}C . D—autoradiograph of lobate tentacle incubated in the dark showing insignificant ^{14}C labelling. Same scale as shown in 2A throughout. ZX—zooxanthellae, e—epidermis, g—gastrodermis, cl— ^{14}C label.

Respiration and photosynthesis

The relative abundance of zooxanthellae in the lanceolate and lobate tentacles of *Lebrunia coralligens* is shown in Figures 2A and B. In the lanceolate tentacles the cells are distributed in a thin layer while in the lobate tentacles they lie densely packed throughout a thick gastrodermal layer. When *L. coralligens* were incubated in $\text{NaH}^{14}\text{CO}_3$ in the light and analysed for incorporation of ^{14}C by tissue autoradiography it readily became apparent that uptake occurred in the zooxanthellae and in the tissue of the tentacles. Radioactivity associated with the zooxanthellae and the anemone tissue was high (Fig. 2C) after 12 h exposure. Control incubations in the dark showed that non-photosynthetic uptake of the ^{14}C by zooxanthellae was negligible (Fig. 2D).

Measurements of oxygen production in whole animals with expanded lobate tentacles showed a net oxygen production. In order to demonstrate that most of the photosynthetic activity occurs in the lobate tentacles, measurements of rates of oxygen production and of respiration were made on anemones in which all the lobate tentacles were first fully expanded and in which half of the tentacles were retracted. Contraction of lobate pseudotentacles was achieved by simply making a small incision in the tip of a tentacle with a pair of fine scissors. The incision caused the lobate tentacle to withdraw and contract. All lobate tentacles treated in this manner remained contracted for several days while uncut tentacles on the same animal were expanded normally. Thus, following the measurement of oxygen production and consumption in fully expanded animals, half of the lobate pseudotentacles on each specimen were incised and rates of production and consumption remeasured the next day. Results of measurements of rates of production and respiration of fully expanded and incised animals are shown in Table I. Production (P gross) rates were significantly higher in whole animals with fully expanded lobate tentacles than in incised anemones with reduced lobate tentacle expansion ($t = 3.21$, $P < 0.01$, from sets of paired observations). Respiration rates were not significantly different between the two groups, indicating that the incision treatment affected production rates only.

Diurnal cycles of tentacle expansion and contraction

The diurnal cycles of expansion and contraction of lobate and lanceolate tentacles of *Lebrunia coralligens* over a seven-day period are shown in Figures 3–5. Under a natural light program (Fig. 3A) less than 2% of the animals expanded their lobate tentacles in the dark and 92–100% were expanded in the light. During the first three

TABLE I

Mean rates (\pm S.D.) of oxygen production (P) and respiration (R) of whole and incised *Lebrunia coralligens* (mg O_2/h)

Whole animals ¹ · (n = 20)		Incised animals ² · (n = 20)	
P ³	R ⁴	P	R
2.94 (± 0.63)	1.76 (± 0.25)	1.94 (± 0.23)	1.88 (± 0.04)

¹ Animals with all lobate tentacles expanded.

² One half of the lobate tentacles in each animal were incised to induce lobate tentacle contraction.

³ P is gross production, i.e., 'apparent' production measured as increase in oxygen concentration in light vials plus measured respiration in the dark. [See McCloskey *et al.*, (1978) and Muscatine *et al.*, (1981) for definitions.]

⁴ R was determined as decrease in oxygen concentration in darkened vials. Decrease in concentrations was 10–15% of initial values.

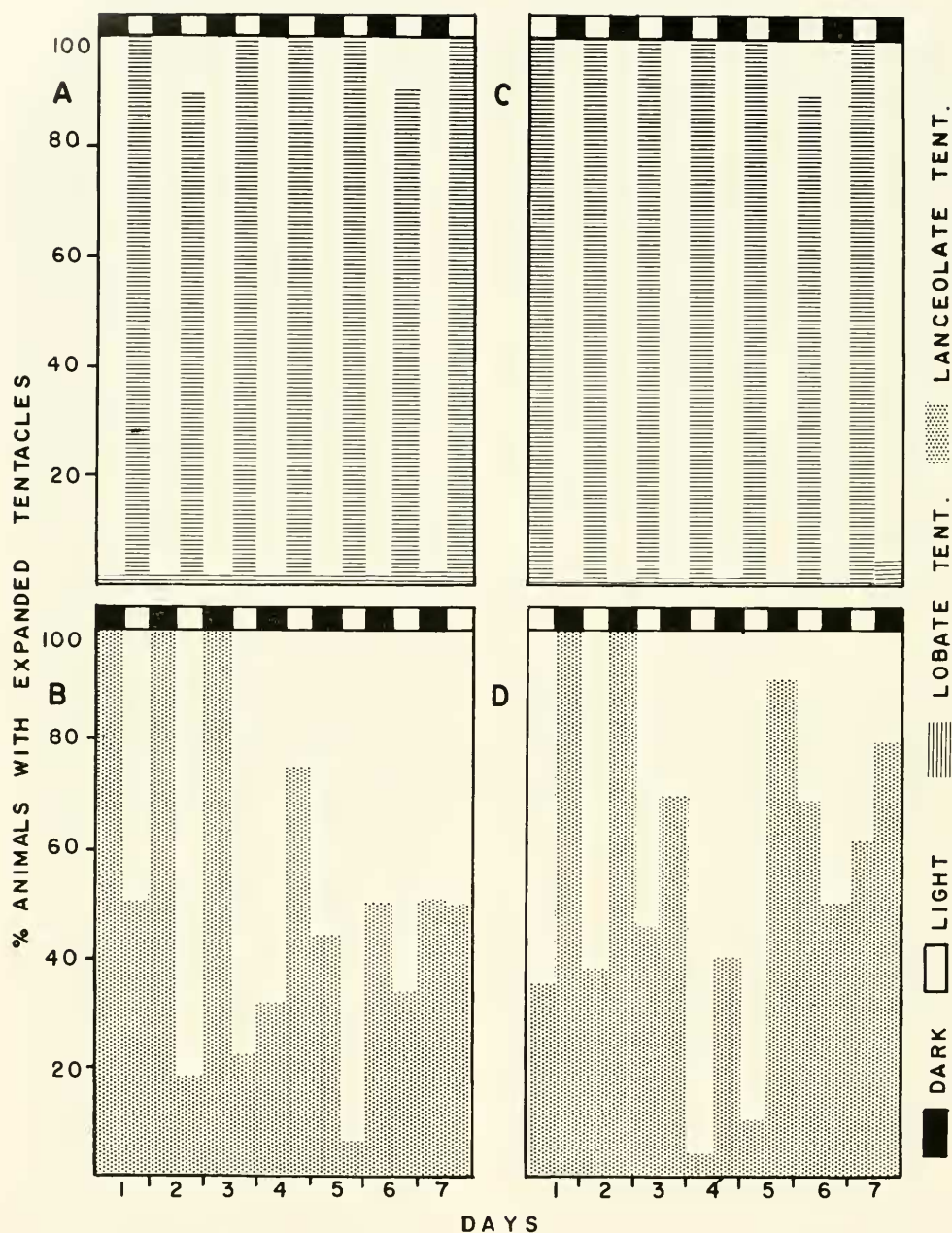


FIGURE 3. Expansion and contraction of tentacles of *Lebrunia coralligens* showing similar responses under natural and reverse 12 h cycles of light and darkness. Animals were fed on first and fourth days. Twenty animals in each group. A—diurnal rhythm of light expansion and dark contraction of lobate tentacles under natural 12 h cycle. B—diurnal rhythm of variable expansion and contraction of lanceolate tentacles under natural 12 h cycle. C—diurnal rhythm of light expansion and dark contraction of lobate tentacles under reverse 12 h cycle. D—diurnal rhythm of variable expansion and contraction of lanceolate tentacles under reverse 12 h cycle.

days lanceolate tentacles (Fig. 3B) were expanded in the dark in all animals but from the fourth through the seventh days lanceolate tentacles were expanded only in 30–50% of animals. In light conditions, the results were highly variable, with lanceolate tentacle expansion occurring in 6–75% of animals.

Under the reversed light cycle experiment (Fig. 3C), lobate pseudotentacles were fully expanded during the light periods in 100% of anemones with the exception of one period (90%). During the dark periods lobate pseudotentacles were fully contracted in 99% of individuals with the exception of one period (95%). Cycles of expansion and contraction of lanceolate tentacles under the reverse light cycle (Fig. 3D) were variable as for the normal cycle. During the first two days lanceolate tentacles were expanded in 100% of anemones in the dark and between 40 and 92% during the following days. Under light conditions expansion of lanceolate tentacles varied between 5 and 70% of anemones.

It is evident then that lobate pseudotentacles responded primarily to the absence or presence of light regardless of the time of day. Lanceolate tentacles were expanded in the dark during the first two or three days but cycles of expansion and contraction were variable thereafter.

In a second pair of experiments, two groups of unfed anemones were exposed to continuous light and continuous darkness for a one-week period (Fig. 4). In animals under continuous light (Fig. 4A) lobate pseudotentacles were expanded in 90 to 100% of animals throughout the seven-day period. Lanceolate tentacles were expanded in 43 to 93% of animals under the conditions of light exposure (Fig. 4B). Thus, as in the 12 h light/12 h dark experiments, the lobate tentacles responded consistently to the presence of light while the lanceolate tentacle response was positive but variable.

Under a regime of continuous darkness (Fig. 4C, D) over the seven-day period only 50% of the unfed animals survived beyond 2.5 days. Nevertheless during each two-day period of activity, lobate pseudotentacles were contracted in 95–98% of anemones and lanceolate tentacles expanded in 15–100% of specimens.

In order to determine the effect of feeding on tentacle behavior, two groups were fed daily with fragments of fish muscle (Fig. 5). Under conditions of continuous light (Fig. 5A) lobate pseudotentacles were fully expanded throughout the seven-day period in 70–100% of anemones, while lanceolate tentacles (Fig. 5B) were expanded in 60–100% of animals. Under conditions of continuous darkness (Fig. 5C, D) 50% mortality of fed anemones occurred every 2–2.5 days. Within each two-day period, lobate pseudotentacles remained 95–98% contracted while lanceolate tentacles were expanded in 10–100% of the animals.

In a comparison of fed and unfed groups of anemones under conditions of continuous light there were statistically significant differences between numbers of animals with expanded lobate and lanceolate tentacles. The number of fed animals with expanded lanceolate tentacles was greater than the number of unfed animals ($t = 3.27$, $P < 0.01$), while the number of fed animals with expanded lobate tentacles was less than unfed animals ($t = 3.23$, $P < 0.01$).

In continuous darkness the high mortality in both fed and unfed groups reduced the data base and prevented any statistical comparison of the two treatments. Lobate tentacles remained unexpanded in both fed and unfed groups while lanceolate tentacle expansion was highly variable.

DISCUSSION

The lobate pseudotentacles of *Lebrunia coralligenes* are photosynthetic organs and are similar to the enlarged bubble tentacles of the scleractinian coral *Plerogyra sinuosa*

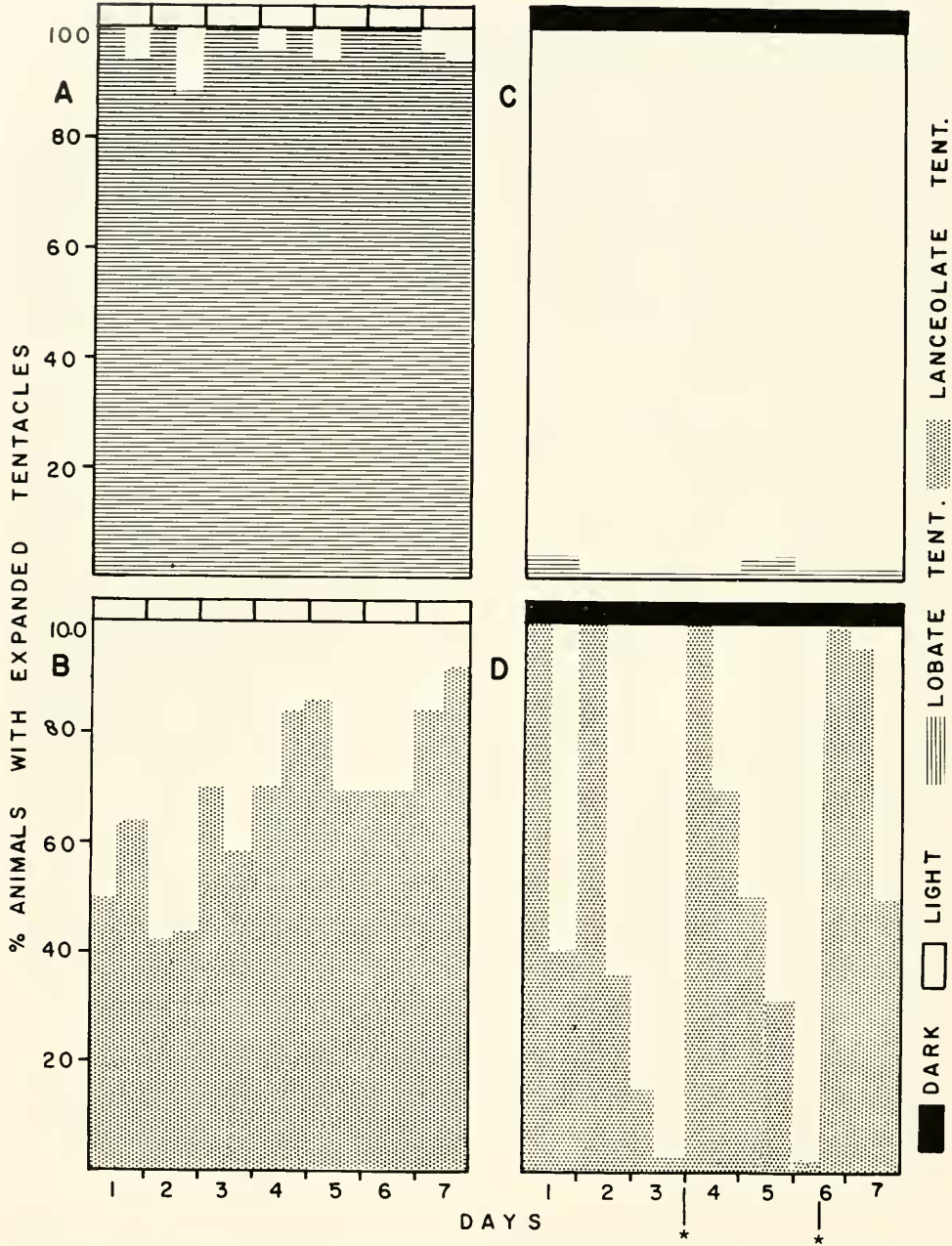


FIGURE 4. Expansion and contraction of the tentacles of unfed *Lebrunia coralligens* showing differences in responses under conditions of continuous light and continuous darkness. Twenty animals in each group. A—expansion of lobate tentacles under conditions of continuous light. B—expansion of lanceolate tentacles under conditions of continuous light. C—continuous contraction of lobate tentacles under conditions of continuous darkness. D—variable expansion and contraction of lanceolate tentacles under conditions of continuous darkness. Asterisks mark time when 50% of animals were dead and whole group replaced.

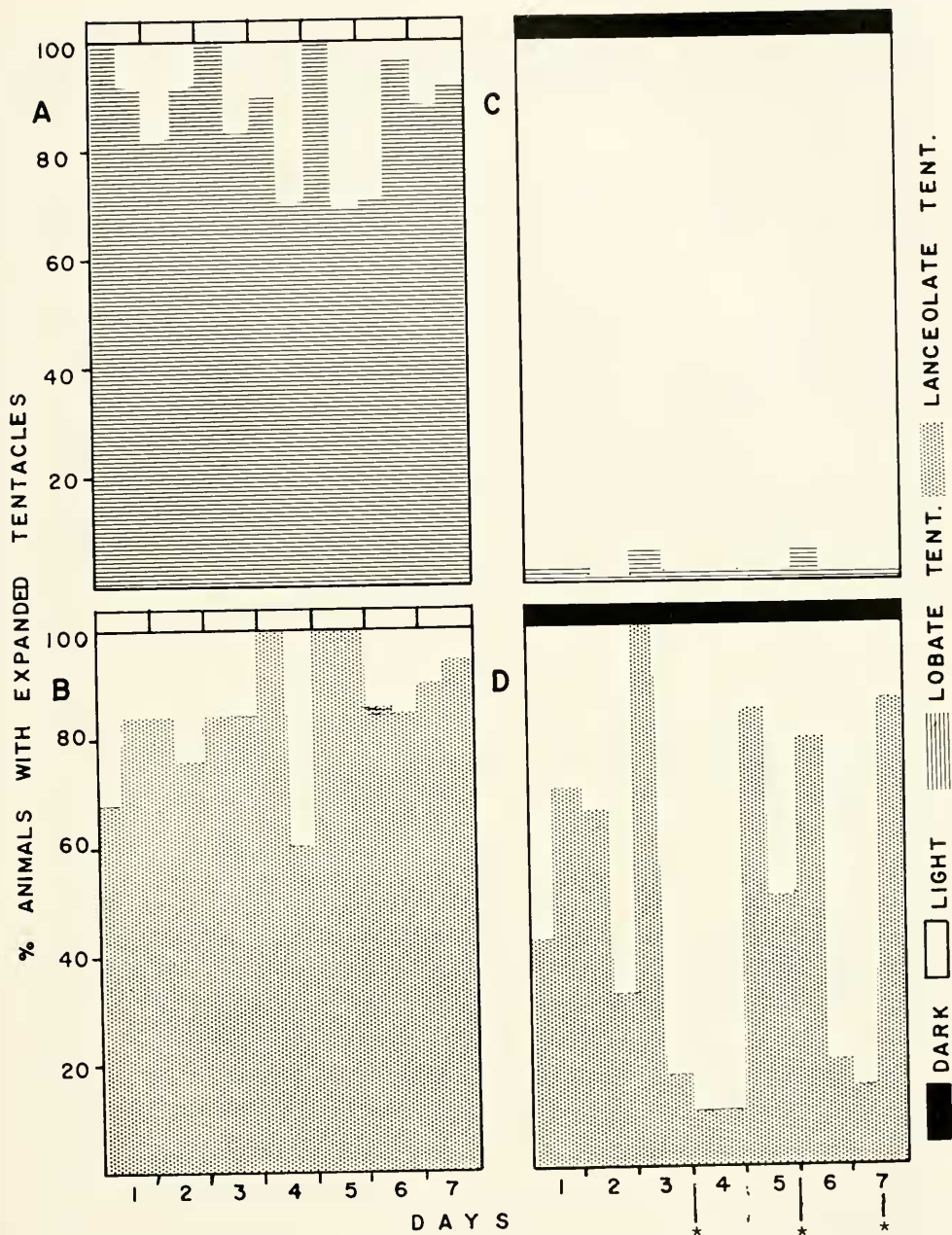


FIGURE 5. Expansion and contraction of the tentacles of *Lebrunia coralligens* fed daily, showing differences in responses under conditions of continuous light and continuous darkness. Twenty animals in each group. A—expansion of lobate tentacles under conditions of continuous light. Number of expanded animals significantly less than in Figure 4A ($t = 3.23$, $P < 0.01$). B—expansion of lanceolate tentacles under conditions of continuous light. Number of expanded animals significantly greater than in Figure 4B ($t = 3.27$, $P < 0.01$). C—continuous contraction of lobate tentacles under conditions of continuous darkness. D—variable expansion and contraction of lanceolate tentacles under conditions of continuous darkness. Asterisks mark the time when 50% of animals were dead and whole group replaced.

as reported by Fricke and Vareschi (1982). A mean gross production to respiration ratio (P/R) for a two hour midday period of 1.67 was determined for *L. coralligens*. This ratio, together with the evidence of translocation of carbon from zooxanthellae to animal tissue, suggests that the anemones may be capable of autotrophy (Muscatine *et al.*, 1981).

The dual nutritional strategy of *Lebrunia coralligens* appears to be reflected in a complex diel rhythm of expansion and contraction. Although sea anemones react to visible light in a variety of ways, the most frequently reported response is contraction (Pearse, 1974). However, a number of anemones which contain zooxanthellae are known to expand during the day and to contract at night (Gosse, 1860; Bohn, 1906; Gee, 1913; Smith, 1939; Pearse, 1974), while others with symbionts show a variety of responses (Pearse, 1974). Sebens and De Riemer (1977) have reported that two other anemones with auxilliary tentacles, *Lebrunia danae* and *Bunodeopsis antillensis*, exhibit the same behavior as *L. coralligens*.

Both in the field (Sebens and De Riemer, 1977) and in the laboratory (Gladfelter, 1975), the lobate pseudotentacles of *Lebrunia coralligens* are expanded in the light and contracted in the dark. The same patterns of expansion and contraction under natural and reversed light/dark cycles in this study support the hypothesis of an exogenous rhythm of activity controlled by ambient light conditions. Furthermore, under the same laboratory conditions, but exposed to continuous light, the lobate tentacles remained expanded for a prolonged period of seven days.

However, light is apparently not the only factor involved, for under conditions of continuous light, anemones which were fed daily showed a significantly lower degree of expansion (number of animals with expanded lobate tentacles) than did anemones without food. This suggests that expansion of lobate tentacles is increased with a lowered nutritional state and decreased when the nutritional state rises above a certain threshold. Thus the unfed animals utilize their lobate tentacles so as to obtain the maximum nutritional intake by autotrophy while fed animals reduce their autotrophic intake.

While it is apparent that the lobate pseudotentacles of *Lebrunia coralligens* expand in the light and contract in the dark in a regular and precise way, the reverse rhythm does not always occur in the lanceolate tentacles. Although Sebens and De Riemer (1977) observed lanceolate feeding tentacles to be expanded at night and contracted during the day in the field, and Gladfelter (1975) found that light contraction and dark expansion would persist for 24 hours, the observed behavior in this study of lanceolate tentacles in the laboratory over a prolonged period was much more irregular and less predictable.

Under natural and reversed light/dark cycles, lanceolate tentacles were expanded in the dark during the first two or three days only and the numbers of expanded animals decreased thereafter. During the same experiment a considerable number of animals were also expanded in the light. Under conditions of continuous light many animals expanded their lanceolate tentacles over a seven-day period.

The variability of the contraction and expansion of the lanceolate tentacles suggests that their behavior is not entirely under the control of ambient light conditions, nor does it occur as a counter response to lobate tentacle condition. Lanceolate tentacles expand under conditions of both light and dark irrespective of whether the lobate tentacles are expanded or contracted. In juvenile *Lebrunia coralligens* without lobate tentacles, the lanceolate tentacles expanded intermittently in both light and dark. Gladfelter (1975) noted that lanceolate tentacles expanded when anemones were disturbed by removing them from the substrate.

Lanceolate tentacle expansion appears to be partly determined by food availability or nutritional state. Under continuous light conditions more fed animals had expanded lanceolate tentacles than did unfed animals. This is in contrast to the behavior of lobate tentacles in which feeding suppressed the degree of expansion. The stimulation of a feeding response by the presence of food in the water is well known in anemones (Reimer, 1970, 1971) and in reef corals (Mariscal and Lenhoff, 1968; Lewis and Price, 1975). The expansion of lanceolate tentacles at night as observed by Sebens and De Riemer (1977) is similar to the nighttime expansion of reef coral polyps (Porter, 1974) which occurs in response to the nighttime increase in plankton (Emery, 1968; Johannes *et al.*, 1970). Nevertheless, Goreau (1956) observed that some colonies of nearly all species of Atlantic reef corals are expanded during the daytime.

The high mortality of anemones under conditions of continuous darkness was an unexpected result. Although Muscatine (1961) found that the anemone *Anthopleura elegantissima* which contains zooxanthellae lost weight rapidly in continuous darkness, specimens remained alive for as long as 12 weeks. It is evident that light is necessary for the welfare of *Lebrunia coralligenes* and possible that the lobate tentacle specialization increases the animal's light dependence.

It is concluded that the behavioral rhythms of the two types of tentacles are integrated by the nutritional status of the animal. The lobate tentacles are photosynthetic organs whose expansion is under the control of ambient light but may be modified by nutritional state. Lanceolate tentacle expansion on the other hand is primarily a feeding response. Thus anemone behavior is an expression of combined nutritional strategies.

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